

A systematic study of three species of *Celleporina* (Bryozoa, Cheilostomata) from Hokkaido, Japan with special reference to their early astogeny

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ABSTRACT—*Celleporina porosissima* and two new species, *C. umbonata* n. sp. and *C. fusiforma* n. sp., from Hokkaido, Japan are described with emphasis on early astogeny. Among its congeners, *C. umbonata* n. sp. is unique in possessing three such characteristics in combination as, a single frontal umbo, a subterminal avicularium on its column, and the avicularian frontal at a right angle to the orifice; *C. fusiforma* is distinct in having the combination of spiramina on frontally budded zooids, a tabula with entire peripheral pores, and pisiform colonies. The three species differ in astogenetic features as follows: The ancestrulae of *C. porosissima* have a budding zone around the distal half from which the first zooid buds off; those of the two new species have a pair of disto-lateral buds from which the first paired zooids bud simultaneously. As the presence of paired zooid buds is assumed to be a synapomorphy, *Celleporina umbonata* n. sp. and *C. fusiforma* n. sp. are considered to be more closely related to each other than to *C. porosissima*.

INTRODUCTION

Members of the family Celleporidae develop multilaminar colonies in which zooids are heaped upon each other. As in the single-layered encrusting species, such multilaminar colonies start with a single encrustation which is formed by repeated budding at the colony margin. Early in their astogeny (ontogeny of a colony), the zooids in the primary layer begin to bud frontally, becoming buried under the secondary layer of zooids thus budded. Subsequently, it is impossible to see any features of the primary layer. Encrusting species of Celleporidae, therefore, have been so far classified according to the morphology of the frontally budded zooids in the outermost layer of colonies. This causes some systematic problems: 1) a limited number of taxonomic characters may make their classification inaccurate or bring a wrong identification; 2) small colonies with a single layer of zooids can not be identified; 3) lack of information on early astogeny makes phylogenetic reconstruction difficult. *Pseudocelleporina triplex* may be the

first celleporid in which early astogenetic changes were fully described to supplement the morphology of mature colonies [19]. However, recent taxonomic studies of *Celleporina*, a large genus of Celleporidae, have still paid attention only to those superficial features [1, 5, 6, 10, 12–14, 21]. Although using modern taxonomic methods such as scanning electron microscopy, they failed to consider any phylogenetic relationships among the congeners.

In Japan, twelve *Celleporina* species including Cenozoic fossils have been reported so far [3, 8, 9, 18, 22–25, 28]. They were described using only the limited characters of the frontally budded zooids, with poor-quality illustrations, so that discrimination between the species is difficult and their phylogenetic relationships are difficult to ascertain.

In Hokkaido, at least three species of *Celleporina* are distributed intertidally. Taking the above-mentioned taxonomic problems into account, we have examined the *Celleporina* species from Muroran and Oshoro-Bay, based on many specimens of various sizes including small colonies obtained by laboratory culture. The present paper deals with the systematics of three *Celleporina*

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species, *C. porosissima*, *C. umbonata* n. sp. and *C. fusiforma* n. sp., of which ancestrulae (first-formed zooid of a colony) and young colonies as well as mature colonies are described in detail by the aid of scanning electron microscopy. The phylogenetic relationships between the three are later discussed in terms of cladistic analysis.

MATERIALS AND METHODS

Celleporid colonies attached to algae were collected during 1990–1991, from the rocky flat, 50 cm deep, near the Oshoro Marine Biological Station, Hokkaido University, Oshoro, and from the intertidal zone on the coast of Muroran. Specimens were carried back to Sapporo and deposited in a seawater-filled aquarium with aeration in the Centre for Experimental Plants and Animals, Hokkaido University.

Specimens of various colony sizes were fixed and preserved in 10% formalin-seawater. They were cleaned with sodium hypochlorite solution, rinsed and dried prior to the observation and measurement under a binocular microscope (Wild M5A type). The dried specimens were coated with gold by an ion sputter (JEOL: JFC-1100E) and observed with the aid of a scanning electron micro-

scope (JEOL: JSM-35 or JSM-5400LV). Cuticular parts were photographed under an optical microscope (Olympus: BH-2), after fixed specimens were decalcified in EDTA or dilute HCl and soaked in sodium hypochlorite solution for a few minutes and mounted with Amman's lactophenol [2] on glass slides with coverslips.

In some live colonies, tentacle number of zooids was counted under a binocular microscope. Some mature specimens were cultured for several weeks to obtain larvae. Larvae released from mature zooids were transferred to small vessels (6.0 cm diameter), in which they were allowed to attach to the inner surface. Development of attached individuals was observed daily. After culturing for nearly two weeks, developed ancestrulae and small colonies with a few zooids were detached from the vessels by soaking in sodium hypochlorite solution. After they were rinsed and dried, the same procedure described above was applied for scanning electron microscopy.

The specimens described here were deposited in the Zoological Institute, Faculty of Science, Hokkaido University (ZIHU), Sapporo.

Before going further, some morphological terms for describing *Celleporina* species should be redefined. Compared with major groups of bryozoans

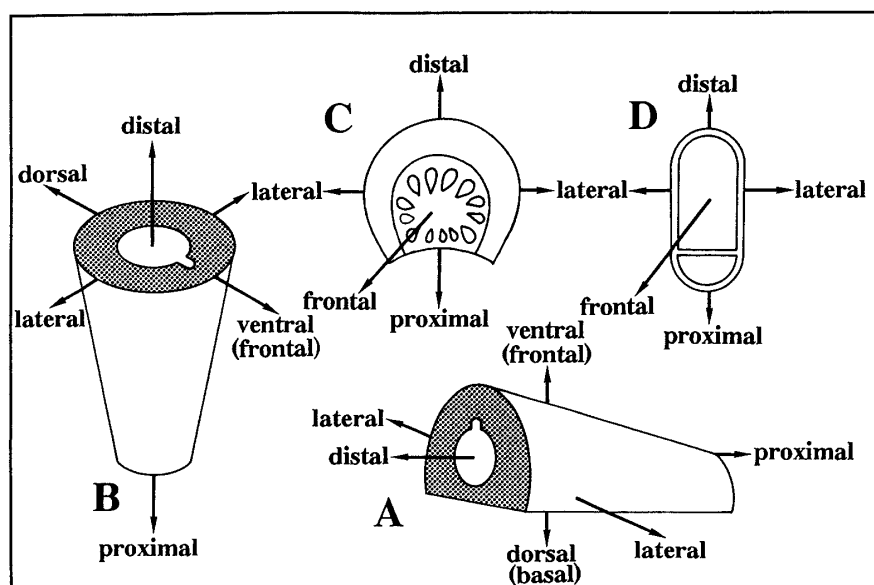


FIG. 1. Schematic diagrams showing the orientation of zooids and their accessories in *Celleporina*. A: A distally budded zoecium. B: A frontally budded zoecium. C: An ovicell. D: An avicularium. Dotted areas indicate the circum-orificial part of the distal zoecial wall.

characterized by having unilaminar colonies, most celleporids have multilaminar colonies with zooids of modified construction and unique orientation of some zooidal features. For example, the term "frontal" may refer to different zooidal orientations in uni- and multi-laminar colonies. Recumbent zooecia in small colonies of *Celleporina* are made by a flat distal wall and a convex frontal shield (Fig. 1A): the former has an orifice at the center surrounded by avicularia and a peristome; the latter has marginal areolae from which "frontal" budding occurs. Repeated frontal budding results in multilaminar colonies, in which most of the zooids are erect or sub-erect and closely packed with each other (Fig. 1B), in which case the venter of one zooid lies under the dorsum of another zooid. The frontal (ventral) wall of each zooid is, therefore, completely concealed between zooids and only the distal walls of zooids are visible from the colony surface, and so the frontal surface of a colony coincides with the distal surfaces of zooids. By contrast, in the zooids of unilaminar species, the frontal surface of zooids coincides with the frontal surface of the colony. Since the morphological terms utilized for bryozoans were created for unilaminar colonies, their application is necessarily restricted to such bryozoans. Therefore such directional terms as distal, proximal, dorsal, frontal, etc. should be used for celleporids more precisely. Our redefinition of these terms for celleporids (Fig. 1) is utilized in the following results in this paper.

In the measurements prior to the description of each species, the following abbreviations are used. L: length; W: width; L/W: length/width ratio; D: depth; N: number; S.D.: standard deviation; NZ: number of zooids; NC: number of colonies.

RESULTS

Genus *Celleporina* GRAY, 1848, char. emend.

Colony multilaminar, massive, encrusting or erect from an encrusting base. Zooids at various stages of development often scattered over the surface of mature colonies, closely packed without clear delimitation, so that only the distal-most part of each zooid is visible at the colony surface. Zooids of two kinds, depending on whether bud-

ded distally or frontally (ventrally): Distally budded zooids recumbent at colony edge; frontally budded ones erect in colony center or sub-erect in the periphery. Zooids subtubular, with a distal zooecial wall almost perpendicular to the frontal wall. The distal wall porous early but later concealed under such accessories as avicularia, peristome, or ovicell. Primary orifice with a ventral sinus at the center of the distal wall. Oral spines absent, at least in frontally budded zooids in mature colonies. Adventitious avicularia and peristome often incorporated into peristomial complex, which encloses secondary orifice. Ovicell hyperstomial, spherical, with a perforated frontal (tabula), not closed by the zooidal operculum. Vicarious avicularia often present.

Celleporina porosissima HARMER 1957 (Fig. 2A-L)

Celleporina porosissima HARMER, 1957, p. 906–907, pl. 62, figs. 3, 16–17 [7]; VOIGT and COOK, 1983, p. 53–55, pl. 1–3 [29].

Material examined. 18 (ZIHU-969-1~18) mature colonies; on the leaves of *Laminaria religiosa* (MIYABE), from about 0.5 m depth on the reef-flat along the western shore of Oshoro-Bay, Otaru, Hokkaido (43°12.4'N, 140°51.7'E), by H. Ikezawa, 28 Aug.1990, 10 Aug.1990. Eight (ZIHU-970-1~8) ancestrulae and 71 (ZIHU-971-1~71) minute immature colonies; 4 Jul.1990, 16 Jul.1990, 10 Aug.1990, 28 Aug.1990, 11 Jul.1991, 30 Jul.1991, remaining data as above.

Measurements. (ZIHU-969-1 except for tentacle number. In mm except for L/W and N.)

		Mean	Range	S.D.	NZ (NC)
Non-brooding zooids					
Primary orifice	L	0.16	0.15–0.19	0.013	10
(with sinus)	W	0.14	0.12–0.19	0.024	10
Sinus	D	0.03	0.02–0.03	0.003	10
Pores around orifice	N	36.2	28–54	8.039	10
Brooding zooids					
Secondary orifice	L	0.23	0.20–0.24	0.015	10
	W	0.18	0.15–0.22	0.020	10
Ovicell	L	0.25	0.22–0.28	0.021	10
	W	0.29	0.24–0.33	0.024	10

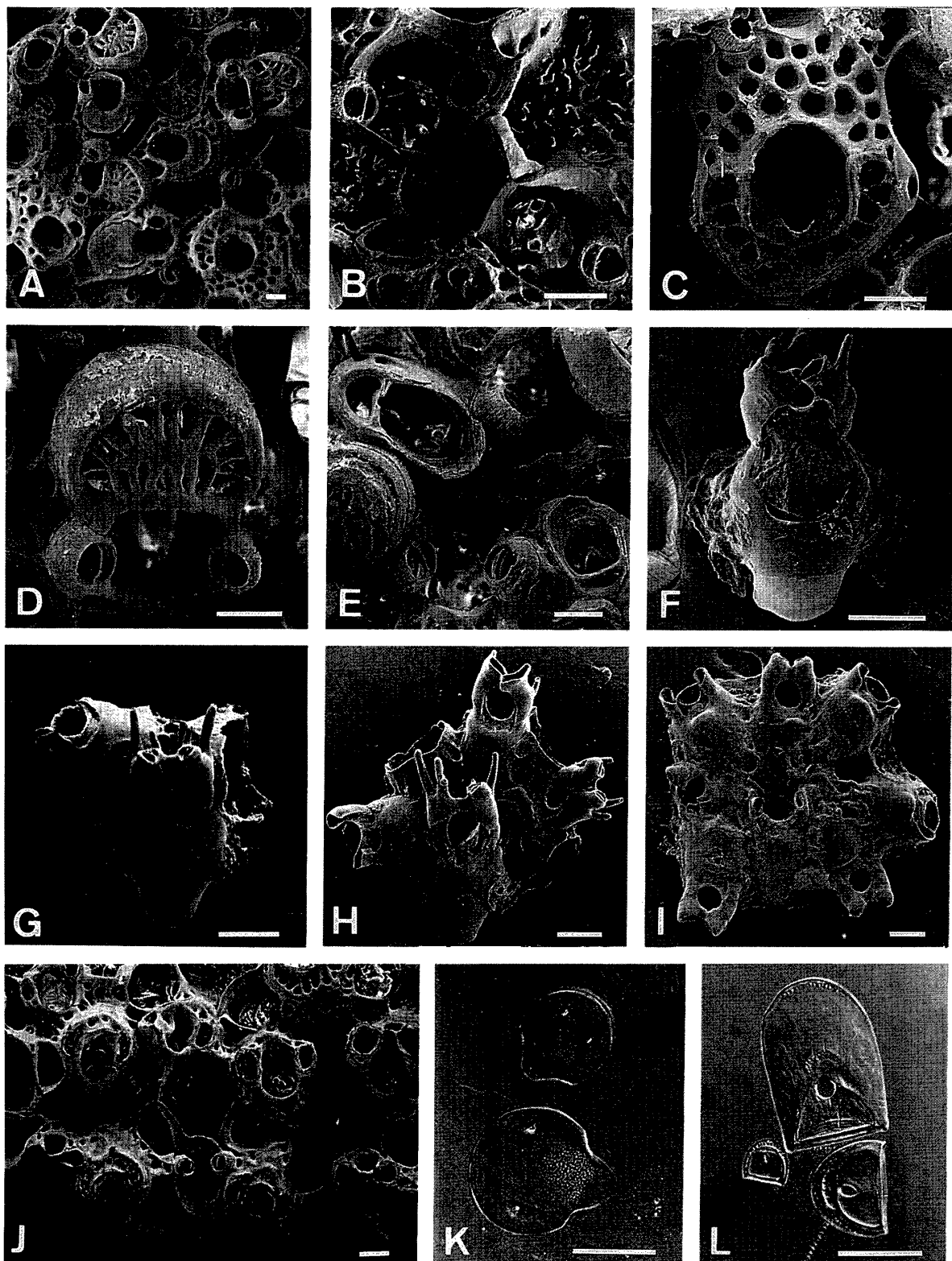


FIG. 2. *Celleporina porosissima* (ZIHU-969-1 for A-E, J; ZIHU-970 for F; ZIHU-971 for G-I; ZIHU-969 for K, L). A: Frontally budded zooids at the central portion of a colony. B: Two types of non-brooding zooids and zooid buds. C: A young zooid with a porous circum-orificial area. D: A brooding zooid with a complete ovicell and adventitious avicularia. E: Two types of vicarious avicularia. F: An ancestrula. G: An ancestrula with a daughter zooid. H: An ancestrula with three peri-ancestrular zooids. I: An ancestrula with seven peri-ancestrular zooids. J: Distally budded zooids at colony edge. K: Two opercula. L: Mandibles of adventitious and vicarious avicularia. Scale bars = 100 μ m.

Tabula	L	0.18	0.17–0.21	0.014	10
	W	0.24	0.20–0.27	0.024	10
Pores on tabula	N	15.4	13–18	1.713	10
Adventitious avicularia					
Palate	L	0.05	0.03–0.07	0.011	10
	W	0.07	0.04–0.13	0.025	10
	L/W	0.70	0.39–0.90	0.145	10
Vicarious avicularia					
Palate	L	0.21	0.18–0.29	0.035	10
	W	0.15	0.13–0.18	0.016	10
	L/W	1.39	1.14–1.95	0.246	10
Tentacle	N	14.0	12–15	0.605	472 (23)

Description. *Skeletal characters* (ZIHU-969-1): Colony encrusting, nearly discoidal, domed, $1.2 \times 1.3 \times 0.15$ cm, orange-colored in life. Colony surface undulated with a lot of low hill-like protrusions, which may be chimneys for exhalation of feeding-water currents.

Non-brooding zooids from frontal budding (Fig. 2A, B) ornamented with a peristome and adventitious avicularia on the distal wall. The avicularia columnar, paired, rarely single (Fig. 2B) or absent. The avicularian columns curved a little, set straight-lateral to the orifice. Both avicularia directed disto-laterally outward; their fronts so slanted that they face disto-centrally, just opposite each other across the orifice. The chamber with a small semicircular terminal palate and a complete pivot bar. Peristome thick and high, forming a tubular peristomial complex in which the paired avicularian columns are incorporated. Primary orifice ovoid, a little longer than wide, with a distinct rounded-V-shaped sinus; situated deeply at the bottom of the peristomial complex, scarcely visible from the colony surface. Secondary orifice enclosed by the peristomial complex, somewhat elliptical, a little wider than long, bilaterally notched by the avicularia.

Non-brooding zooids from distal budding at the colony edge (Fig. 2J) are very similar to those of the frontally budded ones except for some features of the adventitious avicularia. Adventitious avicularia always paired, rarely fused with each other at the sub-terminal ends of the columns to form a bridge and spiramen over the primary orifice. There are no zooids with only a single adventitious avicularium or which lack such avicularia.

Among the zooids at various stages of maturity over the colony surface, young zooids with a porous distal wall are conspicuous and numerous. Young zooids from frontal budding (Fig. 2A, C) with a developed distal wall, of which the part dorsal to the orifice is broad, bearing multiple series of pores, while the ventral side is narrow, with a single row of pores. Adventitious avicularia not developed, otherwise low developing bases of the avicularian columns appear bilaterally to the orifice. Peristome absent. Primary orifice as in non-brooding zooids.

Young zooids from distal budding at the colony edge (Fig. 2J) have the same features as those from frontal budding except the distal wall is reduced, having a single row of pores all around the orifice.

Brooding zooids (Fig. 2A, D) with an ovicell, paired adventitious avicularia and a peristome, collectively concealing the distal wall. Ovicell globose, covered by smooth ectoecium except for the tabula. Tabula large, occupying almost all the ovicell front, variable in shape from nearly semicircular to crescentic, bordered with radially arranged slit- or drop-shaped pores. Adventitious avicularia somewhat stouter than, but of the same shape as, in non-brooding zooids. Peristome high, raised ventrally to the orifice. Secondary orifice nearly rectangular or square in shape, delimited dorsally by the straight proximal edge of the ovicell, ventrally by the peristome, laterally by the avicularia. Primary orifice not visible, concealed deeply under the level of the secondary orifice.

Vicarious avicularia (Fig. 2A, E) scattered frequently over the colony surface, numerous in the center. Palates of two forms: semicircular and large spatulate ones, the latter less frequent. Both types of vicarious avicularia have a complete pivot bar near the proximal end, sometimes with an extensive palatal shelf and a high rostral rim.

Zooid buds (Fig. 2B, J) occur very frequently among the zooids, more numerous in the colony periphery. Spinous processes developed from the inner walls into the coelom of the zooid buds.

Cuticular characters (ZIHU-969-8~18): Operculum (Fig. 2K) variable in size and shape, with two muscular dots and the poster slightly broader

than the sinus which pertains to it.

Mandibles of adventitious avicularia variable in shape, but nearly semicircular, bilaterally symmetrical (Fig. 2L).

Mandibles of vicarious avicularia greatly varying in size and shape and of two types: semicircular and long, large ones, sometimes expanding slightly distally, but almost bilaterally symmetrical (Fig. 2L).

Ancestrulae and astogeny (ZIHU-970, ZIHU-971): Ancestrulae (Fig. 2F-I) schizoporelloid, elongate, slender toward the proximal tip, with a broad budding zone around the distal half from which the first daughter zooid budded (Fig. 2G). Several spines and paired avicularian columns incorporated into a tubular peristomial complex. The columns of paired avicularia stand ventrolaterally to the orifice, and fused with each other at the sub-terminal ends to form a round arch and a large spiramen.

Peri-ancestrular zooids (Fig. 2G-I) almost the same as the ancestrulae in shape, but sometimes lack the peristomial spines and occasionally possess a low umbo on the frontal shield. A few marginal areolae present, from which frontal budding occurs.

Substratum. This species occurs most abundantly on *Laminaria religiosa*, but also on various other kinds of substrata from *Sargassum* spp. and *Rhodoglossum* spp. to molluscan shells in Oshoro Bay. The colonies vary in form depending on the substratum. Domed colonies develop on the flat surface of *Laminaria* fronds or others, while nodular colonies grow around the stem of *Sargassum* spp.

Remarks. *Celleporina porosissima* was originally described by Harmer in 1957 on the basis of material from Japan [7]. The present specimens correspond well with the original description in the following features: 1) dorsally well-developed (multi-porous) distal wall in young zooids from frontal budding (see discussion); 2) primary orifice with long, narrow, distinct sinus; 3) semicircular to crescentic tabula; 4) occasional presence of large vicarious avicularia. Voigt and Cook [29] ex-

amined a paratype and other colonies of *C. porosissima* from Japan in detail and redescribed it with emphasis on the presence of spinous processes within the coelom of zooid buds budded frontally as a new discriminating characteristic. The present specimens also have such spinous processes. The presence of this feature, however, does not discriminate *C. porosissima* from congeners any longer, since it has been reported in *Pseudocelleporina triplex* [19] and is found in the new *Celleporina* species described later in this paper. The present specimens agree with the redescription also in many other points, but differ in the size-ranges of the following characters (the present materials vs. Voigt and Cook's): 1) primary orifice (Length 0.15–0.19 vs. 0.15–0.17, Width 0.12–0.19 vs. 0.11–0.13); 2) vicarious avicularia (Length 0.18–0.29 vs. 0.20–0.25, Width 0.13–0.18 vs. 0.18–0.20). There are no gaps between the size-ranges of the two reports. This does not exclude that the present material belongs to *C. porosissima*.

The ancestrula and peri-ancestrular zooids of the present species are described for the first time. There are two peristomial characters, namely a spiramen and spines, which differ between the mature and peri-ancestrular zooids. The spiramen is present in the ancestrula and peri-ancestrular zooids and, though rare, in non-brooding zooids from distal budding, but completely absent in frontally budded zooids of mature colonies. The spines are present only in the ancestrula and some of the peri-ancestrular zooids. Astogenetic changes will be discussed later in relation to phylogeny.

Celleporina umbonata sp. nov.
(Fig. 3A-L)

Material examined. HOLOTYPE (ZIHU-972-1H): a mature colony; on a leaf of *Rhodoglossum japonicum* (MIKAMI), from the intertidal reef-flat along the shore of Denshin-Hama, Muroran, Hokkaido (42°18.6'N, 140°58.3'E), by H. Ikezawa, 13 Jul.1991. PARATYPES (ZIHU-973-P-1~19): 19 mature colonies, 15 May 1991, 29 May 1991, 15 Jun.1991, 13 Jul.1991, remaining data as for HOLOTYPE. Other materials: 32 (ZIHU-974-1~32) ancestrulae and 18 (ZIHU-975-1~18) minute immature colonies, 15 Jun.1991, 13 Jul.1991, remaining data as for HOLOTYPE.

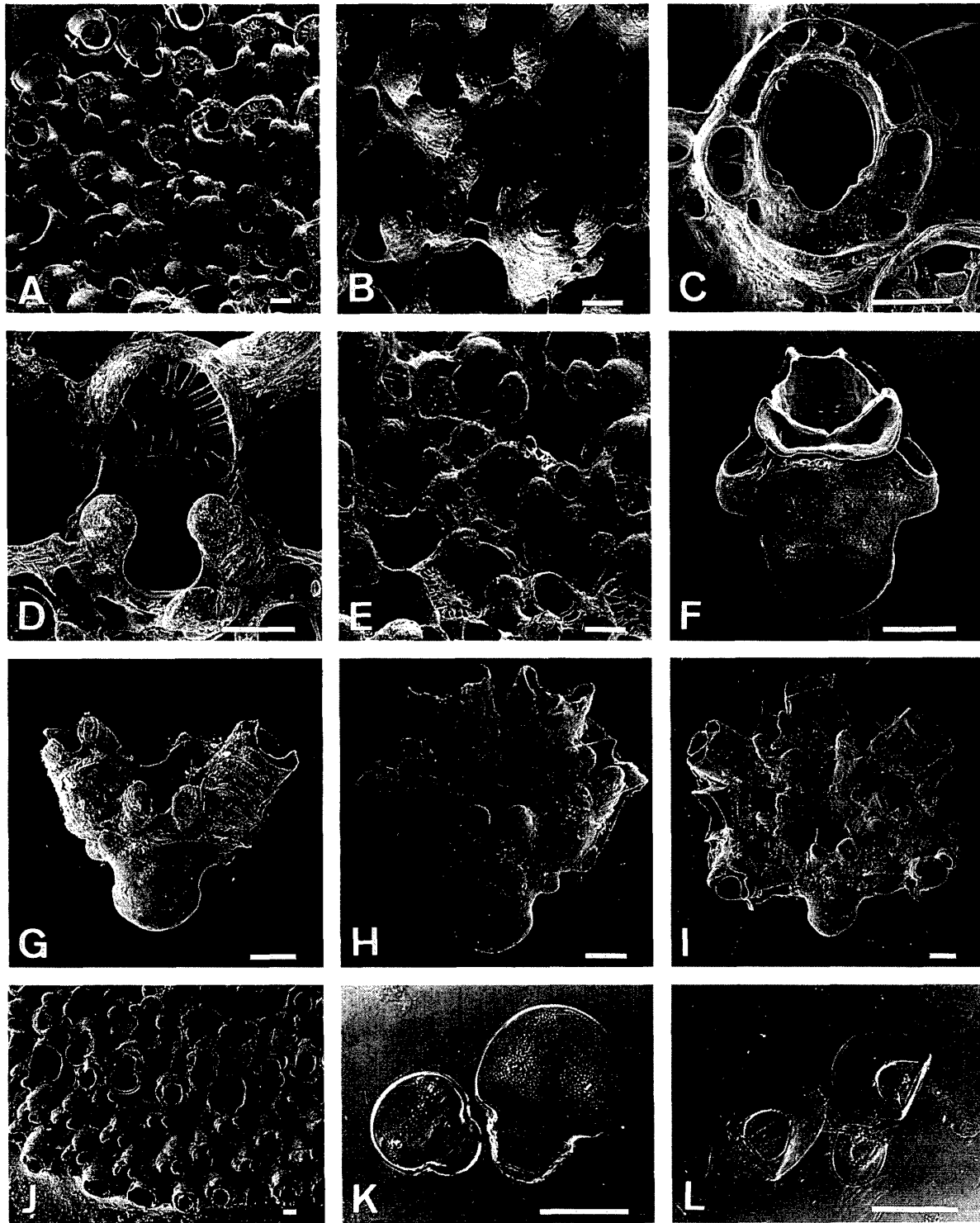


FIG. 3. *Celleporina umbonata* sp. nov. (ZIHU-972-1H for A-E, J; ZIHU-974 for F; ZIHU-975 for G-I; ZIHU-973 for K,L) A: Frontally budded zooids at the peripheral portion of a colony. B: Two non-brooding zooids among some brooding zooids. C: A young zooid with an orifice and pores on distal wall. D: A brooding zooid with a complete ovicell and adventitious avicularia. E: Vicarious avicularia among zooids. F: An ancestrula. G: An ancestrula with two first daughter zooids. H: An ancestrula with four peri-ancestrular zooids. I: An ancestrula with nine peri-ancestrular zooids. J: Distally budded zooids at colony edge. K: Two opercula. L: Mandibles of adventitious and vicarious avicularia. Scale bars=100 μ m.

Etymology. The specific epithet *umbonata* is made of a Latin adjective "umbonatus".

Measurements. (ZIHU-972-1H except for tentacle number. In mm except for L/W and N. Adventitious avicularia are here excluded, since it is impossible to measure their frontals which face closely each other and stand at right angles to the colony surface.)

		Mean	Range	S.D.	NZ (NC)
Non-brooding zooids					
Primary orifice	L	0.15	0.14–0.18	0.018	5
(with sinus)	W	0.13	0.11–0.14	0.012	5
Sinus	D	0.04	0.04–0.05	0.007	5
Pores around orifice	N	13.6	11–16	1.817	5
Brooding zooids					
Secondary orifice	L	0.19	0.17–0.22	0.021	5
	W	0.15	0.15–0.16	0.007	5
Ovicell	L	0.21	0.18–0.25	0.021	10
	W	0.26	0.24–0.30	0.017	10
Tabula	L	0.17	0.15–0.19	0.014	10
	W	0.20	0.17–0.24	0.026	10
Pores on tabula	N	15.6	13–18	1.430	10
Vicarious avicularia					
Palate	L	0.08	0.04–0.11	0.021	10
	W	0.08	0.06–0.11	0.018	10
	L/W	1.10	0.75–1.30	0.154	10
Tentacles	N	11.4	10–13	0.663	411 (22)

Description. *Skeletal characters* (ZIHU-972-1H): Colony encrusting, elliptical, $0.5 \times 0.7 \times 0.1$ cm, colored light orange in life.

Non-brooding zooids from frontal budding (Fig. 3A, B) have a large umbo developed from the frontal wall and a peristomial complex made by adventitious avicularia and a peristome on the distal wall. The adventitious avicularia paired, small, directed distally; each situated at the subterminal end of its column. The avicularian columns long, stout with a blunt tip curved a little inward; somewhat ventro-lateral to the orifice. The avicularian frontals perpendicular to the orifice, somewhat facing each other across the zooecial axis over the orifice, scarcely visible from the colony surface. The chamber with a small semicircular terminal palate and a complete pivot bar. Peristome thin, cylindrical; its frontal part developed in between the avicularian columns, low, with a concave distal margin. The

concave distal margin of the peristome and the central-lateral margin of the parallel avicularian columns smoothly linked together to outline a U-shaped sinus distinct in frontal view. Frontal umbo well developed in the distal direction, long, thick, stout, with a triangular distal tip which frequently covers the peristomial complex frontally. Some space or pores present between the umbo and the peristome front. Primary orifice somewhat ovoid; situated deeply at the bottom of the peristomial complex, scarcely visible from the colony surface. Secondary orifice enclosed by the peristomial complex, round in shape with bilateral notches of the avicularian columns.

Non-brooding zooids from distal budding (Fig. 3J) almost the same shape as those from frontal budding except for the shape of the orifice and the position of the avicularian columns relative to the orifice: The orifice more rounded; the paired avicularian columns set not laterally but ventro-laterally around the orifice, being closer laterally with each other, so that the avicularian frontals do not face each other.

Young zooids from frontal budding (Fig. 3A, C) with distal-wall pores, conspicuous and numerous, having the same morphology as those from distal budding. The distal wall narrow, with a single row of large pores surrounding the orifice, leaving a small non-porous area frontally to the sinus. Adventitious avicularia not developed, otherwise low developing bases of the avicularian columns appear bilaterally to the orifice. Peristome absent. A small umbo sometimes present. Primary orifice ovoid, a little longer than wide, with a large, semicircular sinus. A small distinct cardelle occurs at each blunt-corner of the sinus.

Brooding zooids (Fig. 3A, B, D, E, J) have a complete ovicell, paired adventitious avicularia, and a peristome, all of which are incorporated into a peristomial complex concealing the distal zooecial wall completely. Ovicell globose, covered by smooth ectooecium except frontally. Tabula large, occupying most of the ovicell frontal, variable in shape from nearly semicircular to triangular with blunt corners, bordered with radially arranged slit- or drop-shaped pores. The tabula sometimes reduced in size as the edge is covered under an eave-like ectooecium made by secondary calcifica-

tion. Adventitious avicularia like those of the non-brooding zooids from frontal budding. Frontal umbo often present; only its triangular tip visible. Peristome raised between the avicularian columns, frontally to the orifice. Peristomial complex with a distal U-shaped sinus. Secondary orifice somewhat like a depressed gourd in shape: delimited dorsally by the proximal edge of the ovicell, laterally by the paired avicularian columns, and frontally by the peristome. Primary orifice not visible, concealed deeply under the level of the secondary orifice.

Vicarious avicularia (Fig. 3E) of one morphology, scattered quite frequently over the colony surface, numerous in the central area. Palates somewhat semicircular with a complete pivot bar near the proximal end.

Zooid buds (Fig. 3A, J) occur frequently among the zooids. Spinous processes not detected.

Zooids in various stages of maturity are seen over the colony surface. A complete sequence of ovicell formation can be traced (Fig. 3A, J).

Cuticular characters (ZIHU-973-P-9~19): Operculum (Fig. 3K) with two muscular dots; variable in size and shape, but similar to the orifice in shape.

Mandibles of adventitious and vicarious avicularia variable in size, but constant in shape as almost short-spatulate with parallel sides (Fig. 3L).

Ancestrulae and astogeny (ZIHU-974, ZIHU-975): Ancestrulae (Fig. 3F-I) schizoporelloid, stumpy, rounded proximally, with a pair of distolateral expansions from which a pair of first daughter zooids bud. Other ancestrular features are as for non-brooding zooids from distal budding, but having the avicularian columns standing almost frontal to the orifice. Frontal umbo sometimes developed a little by secondary calcification. Oral spines not detected.

Peri-ancestrular zooids (Fig. 3G-I) almost the same in structure as the non-brooding zooids from distal budding in mature colonies, but the avicularian columns stand more frontally as in the ancestrula, and the umbo on the frontal wall does not develop to reach to the distal margin of peristome,

never covering the frontal surface of the peristome. No oral spines.

Substratum. At Muroran, this new species is found on both *Chondrus yendoi* and *Rhodoglossum japonicum* as discoidal or nodular colonies.

Remarks. Characteristic features of *Celleporina umbonata* sp. nov. include subterminal avicularium on its column and each avicularian frontal at a right angle to orifice. These have been so far reported in *Celleporina fragilis* Arístegui [1]. The present new species differs from *C. fragilis* in having the following features (those of *C. fragilis* in parenthesis): 1) a single frontal umbo (one or two); 2) rugose frontal wall (smooth or granular); 3) many semicircular vicarious avicularia (a few, spatulate); 4) schizoporelloid ancestrulae with no oral spines (tatiform ancestrulae with 5 oral spines). The presence of a frontal umbo has been already recorded in *C. costazii* and *C. costazii* var. *tubulosa* by Hincks [16]. *Celleporina umbonata* sp. nov. is, therefore, unique in having three such characteristics in combination as, a single frontal umbo, a subterminal avicularium on its column, and the avicularian frontal at a right angle to the orifice.

Celleporina fusiforma sp. nov.
(Fig. 4A-L)

Material examined. HOLOTYPE (ZIHU-976-1H): a mature colony; on a narrow stem of *Bossia cretacea* (JOHANSEN), from the intertidal reef-flat along the shore of Denshin-Hama, Muroran, Hokkaido (42°18.6'N, 140°58.3'E), by H. Ikezawa, 13 Jul.1991. PARATYPES (ZIHU-977-P-1~22): 22 mature colonies, 15 May 1991, 29 May 1991, 13 Jul.1991, remaining data as for HOLOTYPE. Other materials: 61 (ZIHU-978-1~61) ancestrulae and 84 (ZIHU-979-1~84) minute immature colonies, 15 May 1991, 29 May 1991, 15 Jun.1991, 13 Jul.1991, remaining data as for HOLOTYPE.

Etymology. The specific epithet *fusiforma* is latinized combination of the English terms "fused" and "form".

Measurements. (ZIHU-976-1H except for tentacle number. In mm except for L/W and N.)

Mean	Range	S.D.	NZ
			(NC)

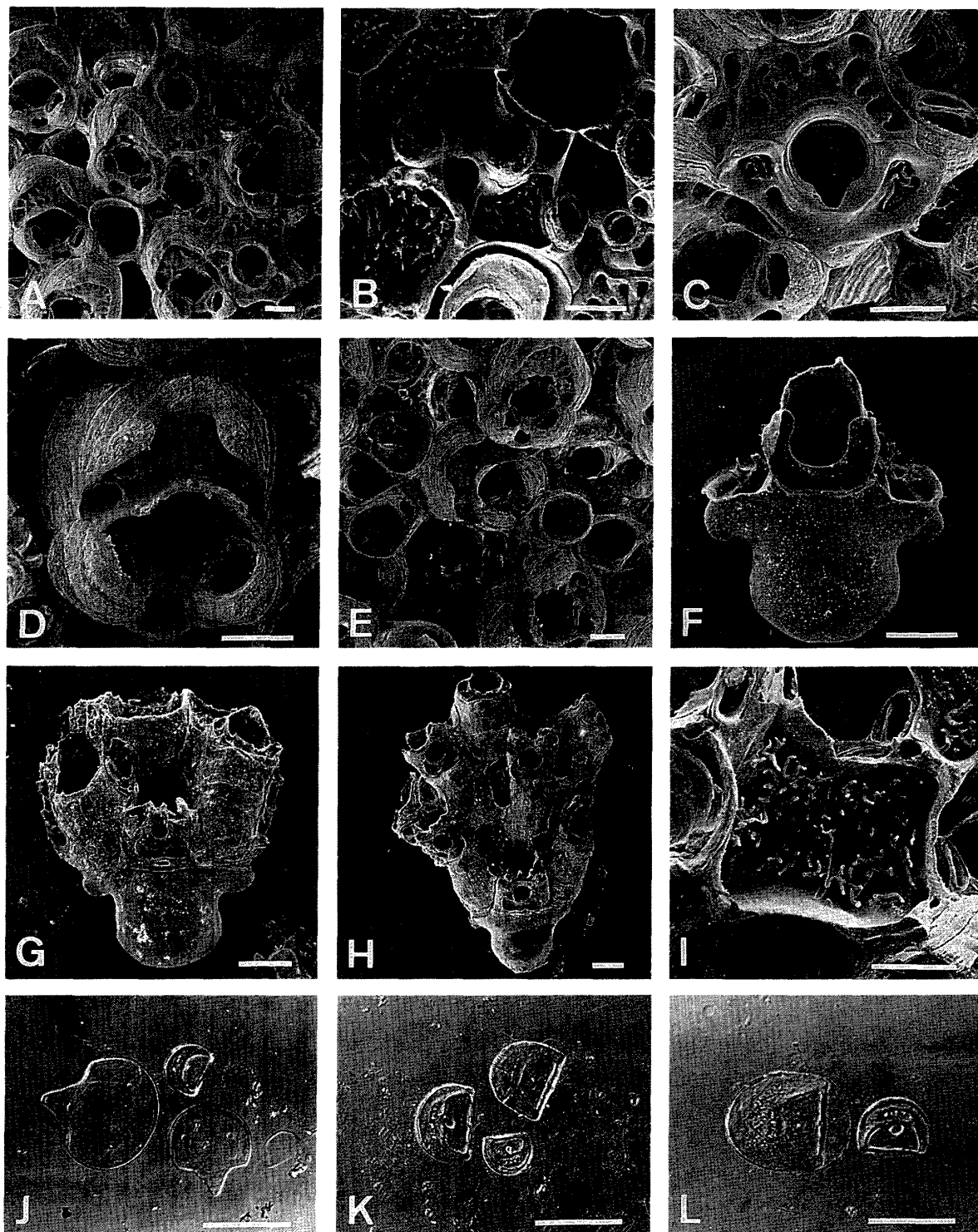


FIG. 4. *Celleporina fusiforma* sp. nov. (ZIHU-976-1H for A-E, I; ZIHU-978 for F; ZIHU-979 for G-H; ZIHU-977 for J-L) A: Frontally budded zooids at the central portion of a colony. B: Two non-brooding zooids and zooid buds C: A young zooid with porous circum-orificial area. D: A brooding zooid with a complete ovicell and adventitious avicularia. E: Vicarious avicularia among zooids. F: An ancestrula. G: An ancestrula with two first daughter zooids. H: An ancestrula with six peri-ancestrular zooids. I: Interior spinous processes in a zooid bud. J: Two opercula and a mandible of adventitious avicularia. K: Mandibles of adventitious and vicarious avicularia. L: Mandibles of two vicarious avicularia. Scale bars=100 μ m.

Non-brooding zooids					
Primary orifice	L	0.12	0.11–0.13	0.008	6
(with sinus)	W	0.11	0.10–0.13	0.008	6
Sinus	D	0.03	0.01–0.04	0.009	6
Pores around orifice	N	18.2	15–24	3.189	6
Brooding zooids					
Secondary orifice	L	0.12	0.10–0.13	0.009	6
	W	0.16	0.15–0.18	0.014	6
Ovicell	L	0.21	0.18–0.27	0.023	9
	W	0.28	0.24–0.32	0.021	9
Tabula	L	0.17	0.14–0.20	0.017	9
	W	0.23	0.15–0.26	0.032	9
Pores on tabula	N	15.3	13–18	1.890	7
Adventitious avicularia					
Palate	L	0.04	0.04–0.05	0.006	6
	W	0.07	0.05–0.08	0.010	6
	L/W	0.63	0.55–0.78	0.093	6
Vicarious avicularia					
Palate	L	0.13	0.07–0.18	0.038	10
	W	0.12	0.07–0.15	0.028	10
	L/W	1.13	0.83–1.56	0.249	10
Tentacles	N	12.0	9–15	0.868	472
(24)					

Description. *Skeletal characters* (ZIHU-976-1H): Colony encrusting, pisiform, surrounding a slender stem of *Bossiella cretacea*, 0.5×0.7 cm, orange-colored in life. Because of the pisiform colony, distally budded zooids are not detected.

Non-brooding zooids from frontal budding (Fig. 4B) rarely present, with a peristome and adventitious avicularia on the distal wall. Adventitious avicularia paired, columnar. The avicularian columns set ventro-lateral to the orifice; short, stout, curving inward, fusing with each other at the sub-terminal ends to form a round arch and a large spiramen over the orifice. The avicularia large, directed obliquely distally outward; their fronts inclined toward each other over the spiramen. The chamber large, with a broad semicircular terminal palate and a complete pivot bar. Peristome thick and high, forming a tubular peristomial complex into which the pair of avicularian columns and spiramen are incorporated. Primary orifice situated deeply at the bottom of the peristomial complex. Secondary orifice enclosed by the peristomial complex, irregular in shape.

Young zooids from frontal budding (Fig. 4A, C) with a developed distal wall, of which the part

dorsal to the orifice is somewhat broad, bearing a few rows of pores, while the ventral side is narrow, with a single series of pores or without any. Adventitious avicularia not developed, otherwise low developing bases of the avicularian columns appear bilaterally to the orifice. Peristome absent. Primary orifice small, circular, with a distinct, sharp V-shaped sinus. A small cardelle occurs at each blunt-corner of the sinus.

Brooding zooids (Fig. 4A, D, E) have an ovicell and paired adventitious avicularia, under both of which the distal wall is completely concealed. Ovicell globose, covered by a thick ectooecium except for the tabular area. Tabula small; its shape variable from crescentic to a somewhat thin meniscus with an irregular outline, delimited distally by the overgrowth of the distal ectooecium and proximally by a raised lip; bordered with radially arranged pores somewhat drop- or elliptically shaped. Adventitious avicularia the same in shape as in non-brooding zooids. Peristome low, narrow, just raised between the avicularian columns ventrally to the orifice, delimiting the proximal edge of a spiramen. Secondary orifice nearly fan-shaped, delimited dorsally by the curved proximal edge of the ovicell, ventro-laterally by the paired avicularia. Primary orifice not visible, concealed deeply under the level of the secondary orifice.

Vicarious avicularia (Fig. 4E) scattered frequently over the colony surface. Palates somewhat semicircular, often expanded slightly distally, with a complete pivot bar near the proximal end, sometimes with a palatal shelf and a high rostral rim.

Zooid buds (Fig. 4B, I) occur very frequently among the zooids. Spinous processes are conspicuously developed from the inner wall into the coelom of zooid buds.

Zooids at various stages of maturity are scattered over the colony (Fig. 4A-E).

Cuticular characters (ZIHU-977-P-10~22): Operculum (Fig. 4J) variable in size, but nearly equal to the orifice in shape, with a sharp V-shaped extension and two muscular dots.

Mandibles of adventitious avicularia (Fig. 4J, K) slightly variable in shape, but nearly semicircular.

Mandibles of vicarious avicularia (Fig. 4K, L) variable in size, but almost semicircular in shape.

Ancestrulae and astogeny (ZIHU-978, ZIHU-979): Ancestrulae (Fig. 4F-H) schizoporelloid, stumpy, rounded proximally, with a pair of small expansions disto-laterally from which the first pair of daughter zooids is budded. A few small spines and paired avicularian columns present, incorporated into a peristomial complex. Avicularian columns short, set almost frontally to the orifice, fused with each other at the sub-terminal ends to form a round arch and a small spiramen. The sinus of the primary orifice a rounded-V shape.

Peri-ancestrular zooids (Fig. 4G, H) tubular, elongated, parallel sided. Paired avicularian columns stouter and longer than those of ancestrulae. Spiramen larger than that of the ancestrula. No frontal spines. A few marginal areolae present. The other zooidal features correspond with those of the ancestrula.

Substratum. This species is frequently collected from the fronds of *Bossiella cretacea* and occa-

sionally *Rhodoglossum japonicum*, *Chondrus pin-nulatus*, and *Gymnogongrus flabelliformis*.

Remarks. Non-brooding zooids from distal budding are excluded from the above description, since they could not be detected from the pisiform colony which surrounded the slender stem of *Bossiella cretacea*. In the present new species, the spiramen made by the union of the paired columns of adventitious avicularia is present even in frontally budded zooids of mature colonies. This has been so far reported only in *Celleporina geminata* in the genus *Celleporina*. *Celleporina geminata* was described originally by Ortmann [26] and periodically redescribed by some other authors, of which Harmer [7] is the most reliable. The present specimens differ from *C. geminata* sensu Harmer in the following respects (Harmer's description in parenthesis): 1) colony pisiform (erect, bifurcating); 2) primary orifice small, circular (long, with nearly parallel sides); 3) tabula with entire

TABLE 1. Differential characteristics between *Celleporina porosissima*, *C. umbonata* n. sp., and *C. fusiforma* n. sp.

Zooid characters	<i>C. porosissima</i>				<i>C. umbonata</i>				<i>C. fusiforma</i>		
	A	P	D	F	A	P	D	F	A	P	F
Two daughter buds from an ancestrula	—				+				+		
Adventitious avicularia											
Paired	+	+	+	+ / —	+	+	+	+	+	+	+
Direction	Obliquely outward				Distally				Obliquely outward		
Face	Disto-centrally				Centrally				Disto-centrally		
Position of columns	Ventro-lateral		Lateral		Almost frontal		Somewhat Ventro-lateral		Almost frontal		ventro-lateral
Shape of orifice	Ovoid				Circular		Ovoid		Circular		
Shape of sinus in orifice	Shapes between U and V				Broad-U-shape				Shapes between U and V		V-shape
Spines	+	+ / —	—	—	—	—	—	—	+	+ / —	—
Spiramen	+	+	+ / —	—	—	—	—	—	+	+	+
U-sinus of peristome	—	—	—	—	+	+	+	+	—	—	—
Pores on distal wall of young zooids	—	+	+	+	—	+	+	+	—	+	+
Dorsal pores on distal wall of young zooids	—	—	—	+	—	—	—	—	—	—	+
Spinous processes in zooid buds	+	+	+	+	—	—	—	—	+	+	+

A: ancestrulae; P: peri-ancestrular zooids; D: distally budded zooids; F: frontally budded zooids; +: present; —: absent; +/-: present or absent.

peripheral pores (with a single distal series of pores); 4) vicarious avicularia somewhat semi-circular (enlarged, spatulate).

DISCUSSION

Distinction of developmental stages of zooids and reconsideration of zooidal characters

Taxonomic characteristics, including those of early astogenetic stages, are compared for the three species in Table 1. Each species has been described here according to precisely defined developmental stages of zooids, namely brooding, non-brooding, and young zooids. The distinction between the non-brooding and young zooids was not necessarily clear in *Celleporina*. For example, in *C. porosissima*, Harmer described and figured the zooids with neither avicularia nor a peristome but with pores around the primary orifice [7, Pl. LXII, Fig. 3]. Zooids of that type are so numerous and conspicuous in the outer-most layer of multi-laminar colonies that they have probably been considered as typical zooids of *Celleporina*. Harmer's style of description had predecessors [22, 24, etc.], and he was followed in this by other authors [29]. These descriptions are, however, neither of typical nor complete zooids but of young zooids in the sense of Osburn (1952), who described *C. robertsoniae*, *C. costazii*, and *C. nordenskjoldi* with illustrations of young zooids [27, Pl. 62, Figs. 2, 3, Pl. 63, Fig. 5]. Mature non-brooding zooids of *Celleporina* have fully developed avicularia and a peristome, which together conceal the circum-orificial pores of the distal wall of young zooids. Since such pores are arranged in different ways among the present species, even young zooids lacking adult features may contribute to *Celleporina* taxonomy. Young zooids are also to be preferred for descriptions of the primary orifice, since mature non-brooding or brooding zooids have a well-developed peristomial complex which conceals the primary orifice.

As another way of more precisely describing zooids of *Celleporina*, we have treated frontally and distally budded zooids separately, since some discrepancies in morphology occurred between these zooids even in mature colonies, particularly

for *C. porosissima* in which spiramina are not detected in frontally but in distally budded zooids. We recommend that future descriptions of other *Celleporina* species follow this format. This is supported by the finding of some characteristics, traditionally overlooked in *Celleporina* taxonomy, which usefully discriminate between the present three species. For example, these species may be distinguished on the basis of the arrangement of the adventitious avicularia, i.e., where do the columns occur around the orifice?; in which direction is the mandible directed?

Cuticular characters, properly introduced into the present descriptions, have likewise been shown to be useful for discriminating species. For example, species-specificity in orifice shape was reinforced by clear differences in the shapes of cuticular opercula.

Voigt and Cook considered the presence of interior spinous processes as specific to *C. porosissima* [29]. Later, Mawatari detected similar ones in the zooids of *Pseudocelleporina triplex* [19]. His findings are endorsed by the present study which found similar processes again in *C. porosissima* and newly in *C. fusiforma*. Consequently, the occurrence of spinous processes is no longer a specific characteristic of *C. porosissima*.

Some characters traditional for *Celleporina* taxonomy proved to be useful again in the present study. Those are 1) presence of spiramen, 2) shape of tabula, 3) number and arrangement of pores on tabula, 4) size and shape of orifice, 5) shape of the sinus of orifice, 6) number and arrangement of pores on the distal wall of young zooids, 7) details of avicularian columns, 8) development of umbo, and so on.

Ancestrulae for cladistic analysis

Taxonomic characters of ancestrulae used in the present study are 1) shape, 2) accessories on distal wall, 3) position and number of buds, and 4) budding angle of first daughter zooids. Ancestrulae have so far been reported in eight species of *Celleporina*: *C. hassallii* [4, 15, 17], *C. bicostata* [11], *C. pinnacula* [11], *C. asymmetrica* [21], *C. conescharellinoides* [6], *C. fragilis* [1], *C. labiata* [1], and *C. lucida* [1]. These species have the

modified type of tatiform ancestrulae with a sub-terminal opesium surrounded by spines, except for *C. conescharellinoides* which lacks spines [6]. The present three *Celleporina* species have ancestrulae of the schizoporelloid type with almost the same features as those of the asexually budded auto-zooids. In *Celleporina*, species with a schizoporelloid ancestrula are regarded as derived, since it is quite probable that such species evolved from a species with a tatiform ancestrula.

Among the present three species, *C. porosissima* has a distinct type of ancestrula which is elongated and slender, with a distal orifice surrounded by spines and a broad budding zone around the distal half from which the first zooid is budded. On the other hand, two new species have a common type of ancestrula which is stumpy and with a pair of disto-lateral buds from which the first pair of daughter zooids bud off simultaneously. The differentiation of distinct disto-lateral buds is common only to the two new species, not having been reported previously in the Celleporidae or even in the Cheilostomata. Therefore, following an outgroup comparison by cladistic analysis, it is determined that the presence of disto-lateral buds is apomorphic. Consequently, the two new species comprise a sister group defined by a synapomorphy, and so they are more closely related to each other than to *C. porosissima* among the three.

Systematic implication of early astogeny

Although relatively few systematic studies have utilized early astogenetic features, recent Japanese research has taken small but steady steps in this direction on *Pseudocelleporina* and *Microporella* [19, 20], followed by the present study on *Celleporina*. Supplementary description of small colonies in the three *Celleporina* species has led to the discoveries of 1) taxonomic characters, 2) characters changeable in astogeny, and 3) early astogenetic characters in distally budding zooids of mature colonies.

The present three species are also distinguished with regard to their later astogeny. *Celleporina porosissima* develops round colonies in which zooids are arranged concentrically with the ancestrula at the center, while the other two species make fan-shape colonies having the ancestrula as

the pivot of the fan. There is a difference in budding angle in the latter two species: larger in *C. umbonata* than in *C. fusiforma*.

Among changeable astogenetic characters of *C. porosissima*, spiramina conspicuously characterize zooids in early astogeny. They also develop in distally budded zooids, though not often, but never in frontally budded zooids in mature colonies. This indicates that small colonies are difficult to identify (even though mature colonies have been fully described). It is also suggested that the characteristics developed in distally budded (but not frontally budded) zooids in mature colonies may be early-astogenetic and primitive.

As stated above, the present study has suggested that early astogenetic data are useful both for the discrimination of *Celleporina* species and for the estimation of their phylogeny. The description of species should, therefore, be supplemented with the features of small colonies. If it is impossible to do so, species should be described with emphasis on the contrasting features of distally and frontally budded zooids. Future comparative investigations on early astogeny of the present three species will make their phylogenetic relationship clearer.

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